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# *Smilax borneensis* (Smilacaceae), an unspecific climbing ant-plant from Borneo and myrmecophytic traits in other Asiatic *Smilax* species

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**Summary.** The monocotyledon climber *Smilax borneensis* A.DC. (Smilacaceae) is a facultative ant-plant that provides both shelter (domatia) and food (extrafloral nectar) for opportunistically nesting ants. The domatia are bladder-like structures at the base of the petiole, facultatively colonised by different arboreal ant genera, e.g., *Crematogaster, Dolichoderus, Technomyrmex* and *Polyrhachis*. Ant occupancy of all studied domatia-bearing plants was 59% (16 of 27 plants), however, the percentage of inhabited domatia per plant varied greatly, ranging from 2.2 to 87.5% (median 8.2, mean 20.0, ± 28.21 SD). Ant nutrition in the form of extrafloral nectar is produced at the tips of growing leaves. Similar domatia structures also occur in several other *Smilax* species, illustrating the potential of the genus *Smilax* for developing associations with ants.

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Ant-plants (myrmecophytes) are conspicuous elements of tropical vegetation. They provide ant shelters (domatia) which vary greatly in their location and morphological development in different plant species (for a review, see Davidson & McKey, 1993). The domatia may be produced from stems, hypocotyl, roots, petiolar structures, stipular structures (including thorns) and leaves. Most of the known myrmecophytes possessing ant-domatia derived

from leaf structures are New World species mainly of the family Melastomataceae (Alonso, 1998; Benson, 1985; Nickol, 1993; Svoma & Morawetz, 1992). In these species, the domatia-forming structure of the leaf is usually at the base of the lamina, as in several species of the genera *Clidemia, Conostegia, Maieta* and *Tococa*. The domatia consist of a pair of adjacent leaf pouches, developed during leaf growth by the invagination of the leaf undersurface. Examples of the Old World are represented by two genera from the African Sterculiaceae, *Cola* and *Scaphopetalum* (Dejean & Djieto-Lordon, 1996), the latter differs from the former by having only a single asymmetrical leaf pouch. Another type of domatia formation by modification of the leaf blade is found in the species of African *Delpydora* (Sapotaceae), *Magnistipula* (Chrysobalanaceae; Letouzey & White, 1976), *Dichopetalum* (Dichopetalaceae, McKey & Davidson, 1993), *Ixora* (Rubiaceae), neotropical *Hirtella* (Chrysobalanaceae; Prance, 1972), *Remijia* (Rubiaceae) and Asian *Callicarpa saccata* (Verbenaceae; Van Steenis, 1967). The basal margins of the leaf blade curl downward, thus providing a cavity for ant nesting. A similar case was found in the Amazonian *Duroia saccifera* Benth. & Hook. f. (Rubiaceae; Wheeler *et al.*, 1929) where leaf margins roll upward. Petiolar ant pouches are known in three species of neotropical *Piper*. Their overlapping petiolar sheaths form a cavity where food bodies are produced and which are colonised by host-specific *Pheidole* ants (Risch *et al.*, 1977). Another type of petiolar ant pouch is found in species of *Pourouma* (Cecropiaceae). In these Amazonian plants, the upper surface of the petiole is strongly depressed and the upward projecting lateral sides of the petiole converge to form a lip-like groove (Benson, 1985). Recently, an Asian heterophyllous myrmecophyte was discovered, *Diospyros andamanica* (Kurz) Bakh. (Wong & Puff, 1995). The opportunistically colonising ant-species on this plant use clusters of small, cup-shaped leaves for nesting. The ant tenants often enlarge the nest space by building carton material around the leaves. The leaf-borne domatia of several epiphytic species of *Hoya* and *Dischidia*, Asian members of the milkweed family (Asclepiadaceae), display great variations, ranging from simple convex plate-like structures (e.g., *Hoya imbricata* Decne.; Merrill, 1946; and *Dischidia collyris* Wall.; Rintz, 1980) to the more complex pitcher leaves of *Dischidia major* (Vahl) Merr. (=*D. rafflesiana* Wall., Treub, 1882) and the ovoid, tightly joint leaf clusters of *Hoya mitrata* Kerr (Weissflog *et al.*, submitted).

These few examples provide evidence for the potential of many foliar structures to be modified into ant shelters. These domatia, however, are known to occur nearly exclusively in dicotyledon plants. Exceptions are observed in monocotyledon rattan palms. The myrmecophytic species of the genus *Korthalsia* possess domatia which are formed by an extension of the leaf sheath beyond the base of the petiole (Dransfield, 1979 and 1984; Mattes *et al.*, 1998).

Here, we describe (i) a new variation in domatia formation by a monocotyledon climber, *Smilax borneensis* A.DC. (Smilicaceae) (ii) the occupancy rate of these domatia (thus assessing their role in forming associations with ants), and (iii) myrmecophytic traits in other members of the genus *Smilax*. The general phenomenon that "ant-plants" rarely

possess ant shelters derived from stipules (or analogous structures) in comparison to plants having domatia borne by leaf lamina or stem is discussed.

## MATERIALS AND METHODS

**The study site.** The field study was conducted in the surroundings of Poring Hot Springs, Kinabalu Park, Sabah, Malaysia (6°03'N 116°41'E). The climate is perhumid and mean annual rainfall ranges from 2000 to 3800 mm. Most of the plants investigated were found in a flat open area near Poring Hot Springs, which was used as cow pasture and orchard, about 500 m above sea level. The area was covered with grass, shrubs such as *Melastoma malabathricum* (Melastomataceae), *Chromolaena odorata* (Asteraceae) and different fruit trees like mango, durian or rambutan and other small trees. A few *Smilax* plants were found at site within the National Park which was covered by evergreen broad-leaved forest, near Langanan Waterfall at 800 m a.s.l. close to the river banks.

**The study species.** *Smilax borneensis* is a monocotyledon climber which seems to be rather common in gaps of primary hill forests as well as in cultivated open land such as orchards and cow pastures in Sabah, Malaysia (Fig. 1). It has also been reported to occur in Central East Borneo and in Sumatra. The genus comprises *c.* 300 species world-wide and *c.* 44 species in SE Asia (Dahlgren *et al.*, 1985; Koyama, 1960). The attachment to the host plants is by means of tendrils which are inserted in pairs on the petiole immediately above the apex of the leaf sheaths. The short prickly thorns which cover the stems and side branches also assist in climbing. The alternate leaves are petiolate and possess a large lamina up to 35 cm long and 28 cm wide. The laminae are 7-nerved, broadly cordate, stiff and coriaceous. The lower surface of the leaf is densely tomentose.

There has been a great deal of controversy about the leaf morphology of *Smilax* species, probably due to the "dicotyledon-like" appearance of petiole and leaf. Especially the often wing-like appendages of many *Smilax* species (forming the myrmecodomatia in *S. borneensis*) at the base of the petiole were considered to be "lateral stipules" (Glück, 1901) or "petiolar wings" (Burck, 1891) or "petiolar sheaths" (Koyama, 1960). Here we follow the terminology used by Domin (1911) who identified these appendages as a derivative of the leaf sheaths. *S. borneensis* grows frequently in clumps, indicating that groups of stems may be vegetative offshoots (ramets) and not genetically distinct plants (genets). However, for our purpose we define an "individual" as a liana stem with its own root system. The stems of this plant have numerous side branches. We could observe branch lengths up to 8 m. The branches could grow much longer but we were not able to pull them down as they were attached to the vegetation. Plants which grow partly on the ground, on shrubs and on small trees were measured (length and diameter), and all domatia were counted and thoroughly checked for their ant inhabitants. Nectar secretion was tested by using insect tangle trap (tangle foot®). The droplets collected were tested for sugar content with Dextrostix (Merck®)

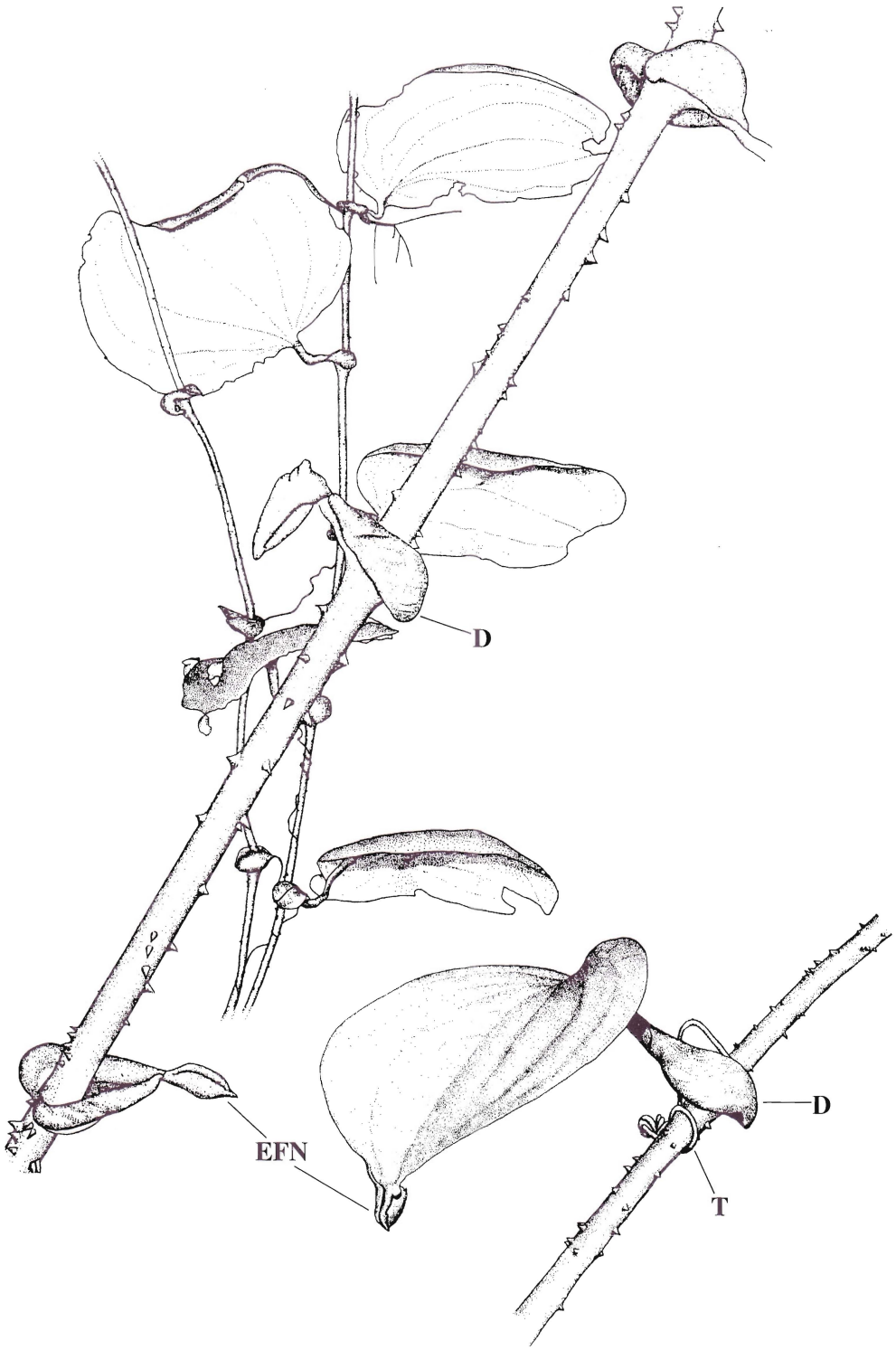


**Fig. 1**. *Smilax borneensis*, showing both domatia and leaves along the stem axis. (D= domatia, EFN= extra-floral nectary, T= tendril).

**Herbarium study.** The following 59 Asian *Smilax* species were checked in the Rijksherbarium Leiden (The Netherlands) for myrmecophytic traits:
*S. adhearens* Gagnep., *S. amboinensis* Back., *S. amplyobasis* Krause, *S. anceps* Wild., *S. annulata* Warb., *S. arisanensis* Hayata, *S. aspera* L., *S. aspericaulis* Wall., *S. australis* R. Br., *S. blumei* A.DC., *S. borneensis* A.DC., *S. bracteata* Presl., *S. calophylla* Wall., *S. china* L., *S. corbularia* Kunth., *S. davidiana* A.DC., *S. elegantissima* Gagnep., *S. elmeri* Merr., *S. elongata-umbellata* Hayata, *S. extensa* Wall. ex A.DC., *S. ferox* Wall. ex Kunth., *S. gagnepainii* T. Koyama, *S. gigantea* Merr., *S. glabra* Roxb., *S. glauco-china* Warb., *S. glaucophylla* Klatzsch, *S. hemsleyana* Craib, *S. hypoglauca* Benth., *S. inversa* T. Koyama, *S. kaniensis* Krause, *S. kingii* Hook.f., *S. laevis* Wall., *S. lanceifolia* Roxb., *S. leucophylla* Bl., *S. lunglingensis* Wang & Tang, *S. luzonensis* Presl., *S. mairei* Lev., *S. marcocarpa* Bl., *S. megacarpa* A.DC., *S. menispermoidea* A.DC., *S. micrantha* (Bl.) Bakh. f., *S. microphylla* C.H. Wright ssp. *elongata* (Warb.) T. Koyama, *S. minutifolia* A.DC., *S. myosotiflora* A.DC., *S. myrtillus* A. DC., *S. novo-guineensis* T. Koyama, *S. ocreata* A.DC., *S. odoratissima* Bl., *S. orthoptera* A.DC., *S. osmastonii* Wang & Tang, *S. ovalifolia* Roxb., *S. ovato-lanceolata* T. Koyama, *S. perfoliata* Lour., *S. polyacantha* Wall. ex Kunth., *S. prolifera* Roxb., *S. riparia* A.DC., *S. setosa* Mig., *S. sinclairii* T. Koyama, *S. zeylanica* L.

All specimens were checked for the presence of domatia and signs of previous colonisation.

## RESULTS

**Domatia.** The leaf sheath of *Smilax borneensis* clasps the stem and develops wing-like appendages with free margins which curl down to either side of the petiole and form two chambers. Upon reaching the stem below the folded sheath curls up again, thus giving rise to a very conspicuous, solid, ovate-acute domatium which encloses the stem from all sides except for a slit of variable size at the points where the folded leaf sheath is not tightly appressed to the stem. Usually the slit, through which the ants gain access into the interior, is found at the lower posterior part of the domatium where the sheaths from either side meet and enclose the stem, opposite to the petiole insertion (Fig. 2). The interior of the domatium is partly divided into two chambers which are longitudinally separated by the petiole in the middle and the axillary bud. Mature domatia are hard-walled, persistent structures that reach a length of up to 5.5 cm (median 4, n=10), the width of each chamber may reach a maximum of 2.0 cm, whereas the height sometimes exceeds 3 cm (median 2.25, n=10). It appears that plants growing in pasture land tended to have somewhat smaller domatia than plants growing in forest.

Only older and larger plants with several branches develop inhabitable domatia at their leaves (Fig.1). Domatia development appears to be correlated with stem diameter rather than stem length. The first fully developed domatia were found in stems with a minimum diameter of 1.3 cm (mean 1.75, ± 0.39 SD; Table 1), usually from the 5th to 7th leaf sheath

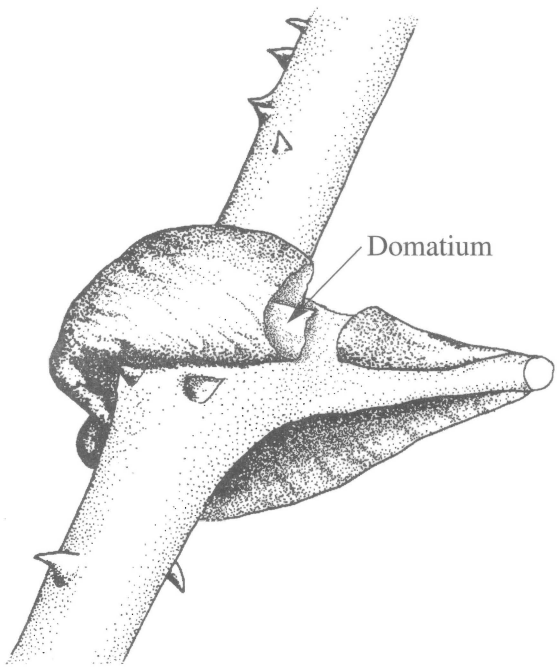


**Fig. 2**. Partly opened domatium of *Smilax borneensis*. Arrow indicates ant entrance.

onwards (counted from the base towards the apex) in a height of *c.* 1–1.5 m. Thinner stemmed plants (<1.2 cm), even up to 4 m in length, lacked domatia, their leaf sheaths did not form closed chambers (n=16; mean stem diameter 0.8 cm, ± 0.27 SD). In domatia-bearing stems, the lowest mature leaf sheaths developed neither domatia nor leaf blades (as shown in Fig. 3).

The appearance of domatia in *S. borneensis* exhibited a considerable variation. In two plants (#26 and #27, see Table 1), the domatia were too small to be colonised by the medium-sized inhabitants, or inhabitable ant-house structures were lacking at all (n=16, Fig. 4). Moreover, 22% of the domatia-bearing plants (6 of n=27; #2, #4, #5, #9, #12, #18, see Table 1) had a considerable portion of their domatia destroyed by herbivores or predators of ants and/or their brood. The damaged domatia remains were often found to be utilised as shelters by cockroaches and spiders.

**Ant inhabitants.** During our study at Poring Hot Spring, we found 43 *S. borneensis* plants in total (Fig. 4). Sixteen plants were without domatia and of the remaining 27 domatia-bearing *Smilax*, 59% (n=16) were colonised by ants (Table 1). The domatia-bearing, but uncolonised plants (n=11) were younger and had fewer domatia (median 23, mean 22.8, ± 9.25 SD) than the inhabited plants (median 39.5, mean 42.3, ± 37.44 SD), however, the difference between number of domatia is not significant (Mann-Whitney U test). On the ant-colonised plants, the ant occupation percentage of the inhabitable domatia varied greatly, ranging from 2.2 to 87.5% (median 8.2, mean 20.0, ± 28.21 SD; see Tab. 1).

The plant were inhabited by 18 species of ants from six genera (*Dolichoderus, Polyrhachis, Technomyrmex, Crematogaster, Camponotus,* and *Strumigenys*). Up to 4 ant species were found nesting within single plant specimen (plant #2, see Table 1). Some *Polyrhachis, Technomyrmex* and *Dolichoderus* species used carton material to enlarge the nesting space or to narrow the entrance of the domatia. In many domatia ant-brood and detritus could be found. Trophobiotic hemipterans were never found inside the chambers.

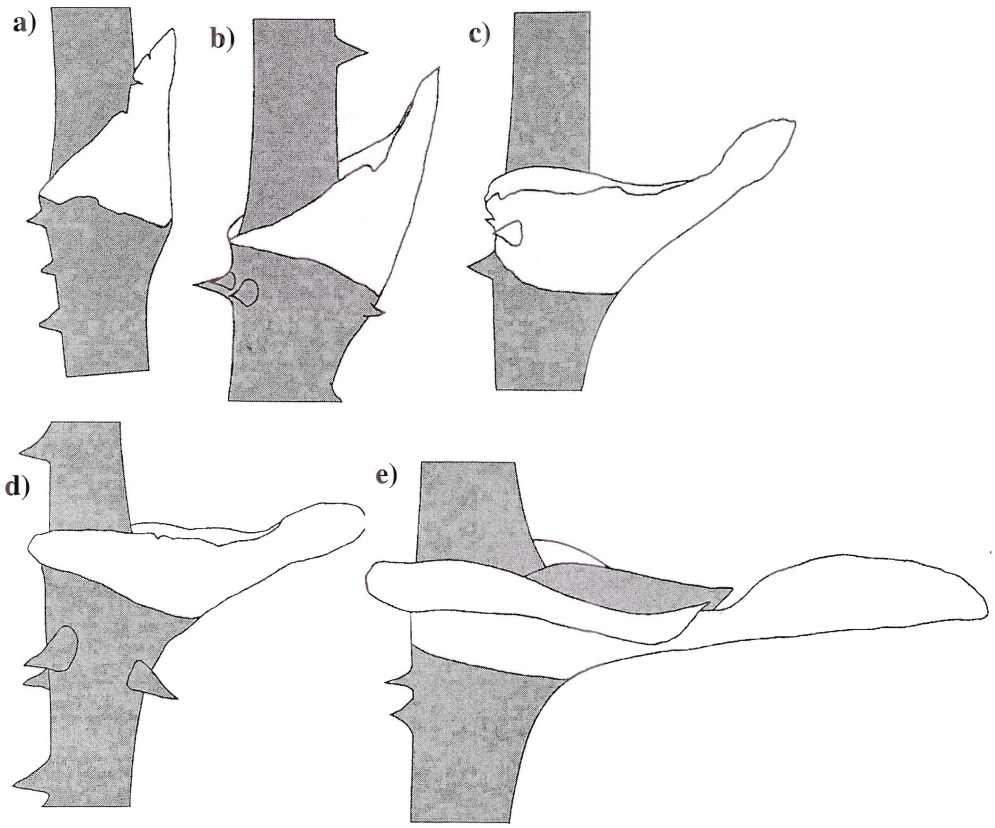


**Fig. 3**. Fully developed leaf sheaths at different positions along the stem of *Smilax borneensis* from a) the lowest to e) the highest.

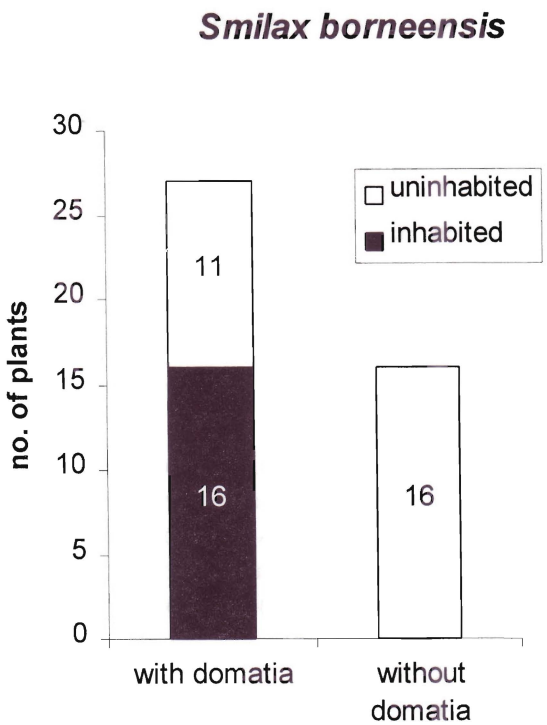


**Fig. 4**. Plant categories (with and without domatia) and their respective frequency of ant occupation.

**Nectar secretion.** In many SE Asian *Smilax* species, including *S. borneensis*, glands at the apex of young developing leaves secrete extrafloral nectar which is readily consumed by visiting ants (Burck, 1891; pers. observation). In *S. borneensis* nectar droplets developed to a visible size 5 minutes after ant removal, and these droplets, tested after 30 minutes of nectar accumulation on a sunny day at around noon, contained at least 2.5 g/l glucose (maximum reading of the quick test). The taste was also clearly sweet. Nectar secretion was observed both in young developing leaves with reduced and with normal developed laminae. Secretion of nectar ceased with maturation of the leaves. Burck (1891) reported that the tips of fully developed leaves wither and fall off. We also observed both in the field and in herbarium specimens that in dozens of mature leaves the apices with the nectar glands were broken off (Fig. 1). However, the causes for this phenomenon are unknown to us.

**Herbarium investigation of *Smilax* species.** From 59 *Smilax* species checked in the Leiden herbarium, 54 did not show any sign of ant inhabitable structures, i.e., they were either lacking such structures or possessed leaf sheaths that appeared to be unsuited for ant colonization. Five species, listed below, had leaf sheaths that formed chambers (n = number of specimens examined):

*S. borneensis* A.DC. (Malaysia: Sabah; n=16): Of all plant specimens studied 69% (n=11) displayed ant-housing structures as described above: persistent, hard-walled leaf sheaths curled down to form a domatium. In one specimen former ant inhabitation was indicated by remains of ant carton found inside a domatium. Apices of mature leaves were often lacking whereas leaf tips of young intact leaves typically turned blackish.

*S. gigantea* Merr. (Borneo; n=11): This plant develops domatia that are very similar to those of *S. borneensis* both in form and size (lengthmedian 3 cm). Of the 6 specimens possessing domatia (55%) one showed remains of a carton nest.

*S. ocreata* A.DC. (India: Assam, Thailand; n=4): All 4 specimens studied had enclosed hollow structures suitable for ant inhabitation. The persistent domatia ($length_{median}$ 2.6 cm, $height_{median}$ 1.0 cm; n=9) were smaller and much more soft-walled compared to those of *S. borneensis*. Another remarkable difference from *S. borneensis* exists: the small-sized *S. ocreata* produces domatia in stems with a diameter of 0.2 cm (median 0.34; n=6).

*S. perfoliata* Lour. (India, Thailand; n=5): All specimens were found to possess ant-house structures, but most domatia (n=20) were formed by *upward* curled sheath margins, whereas 9 leaf sheaths were folded downwards. It is not known the cause of this difference in domatia formation. The rather soft-walled chambers are similar in size to those of *S. ocreata* ($length_{median}$ 2.5 cm, $height_{median}$ 1.2 cm; n=3). One specimen had 4 domatia in which the remains of *Dolichoderus* ants could be found.

**Table 1.** Listed are all studied domatia-bearing *Smilax borneensis* climbers (number of plants=27). Plant length, stem diameter and the total number of domatia per plant are given. [Leaf sheaths which were not fully developed to form a domatium are not included.] For ant-inhabited plants (number of plants=16) the percentage of inhabited domatia and the ant species are added. Asteriks* indicate plants in which one or a few branches were not accessible for us throughout their entire length, thus not all domatia could be counted and checked for ant occupation. Brackets () denote domatia which had, though mature, an unusually small size and were too small to harbour the medium-sized ants commonly found inside the chambers.

| Plant no. | plant length [m] | stem diameter [cm] | total number of domatia/plant | percentage of domatia inhabited by ants [%] | ant species |
|---|---|---|---|---|---|
| #1 | 13.5 | 1.4 | 64 | 3.1 | *Polyrhachis* sp. 3 |
| #2 | >10.0 | 24 | 156* | 14.7 | *Technomyrmex* sp. 1 |
| | | | | | *Technomyrmex* sp. 2 |
| | | | | | *Camponotus* sp. 1 |
| | | | | | *Strumigenys* sp. 1 |
| #3 | 8.6 | 1.7 | 61 | 3.3 | *Dolichoderus* sp. 4 |
| #4 | 6.2 | 1.9 | 45 | 2.2 | *Technomyrmex* sp. 3 |
| #5 | 6.0 | 2.2 | 43* | 2.3 | *Technomyrmex* sp. 3 |
| #6 | 5.3 | 1.8 | 36 | 2.8 | *Crematogaster* sp. 2 |
| #7 | 5.2 | 2.1 | 52* | 9.6 | *Technomyrmex* sp. 1 |
| | | | | | *Technomyrmex* sp. 2 |
| | | | | | *Camponotus* sp. 1 |
| #8 | 5.1 | 2.0 | 14* | 57.1 | *Dolichoderus* sp. 3 |
| #9 | 4.1 | 2.2 | 51 | 3.9 | *Crematogaster* sp. 1 |
| | | | | | *Polyrhachis* sp. 2 |
| #10 | 4.0 | 1.3 | 15* | 6.7 | *Polyrhachis* sp. 1 |
| #11 | 3.3 | 1.4 | 21 | 4.8 | *Dolichoderus* sp. 6 |
| #12 | 3.1 | 2.2 | 75* | 13.3 | *Dolichoderus* sp. 1 |
| | | | | | *Polyrhachis* sp. 4 |
| #13 | 3.0 | 1.4 | 10* | 80.0 | *Dolichoderus* sp. 2 |

| Plant no. | plant length [m] | stem diameter [cm] | total number of domatia/plant | percentage of domatia inhabited by ants [%] | ant species |
|---|---|---|---|---|---|
| #14 | 3.0 | 1.4 | 18 | 16.7 | *Dolichoderus* sp. 5 |
| #15 | 2.7 | 1.3 | 8* | 87.5 | *Dolichoderus* sp.1 |
| #16 | 1.7 | 1.3 | 8 | 12.5 | *Camponotus* sp.2 |
| #17 | 8 | 2.3 | 12 | - | uninhabited |
| #18 | 5.2 | 1.6 | 39 | - | uninhabited |
| #19 | 4.6 | 1.5 | 25 | - | uninhabited |
| #20 | 4.4 | 1.5 | 35 | - | uninhabited |
| #21 | 3.9 | 1.5 | 27 | - | uninhabited |
| #22 | 3.5 | 1.4 | 28 | - | uninhabited |
| #23 | 3.4 | 1.5 | 23 | - | uninhabited |
| #24 | 2.9 | 1.3 | 19 | - | uninhabited |
| #25 | 2.8 | 1.2 | 20 | - | uninhabited |
| #26 | 1.8 | 1.3 | (11) | - | uninhabited |
| #27 | 1.5 | 1.2 | (12) | - | uninhabited |

**Table 2.** *Smilax borneensis* climbers (n=16) lacking ant-housing structures (domatia). Plant length and stem diameter are given.

| Plant no. | Plant length [m] | Stem diameter [cm] |
|---|---|---|
| #28 | 4.0 | 1.2 |
| #29 | 2.5 | 1.0 |
| #30 | 2.5 | 0.8 |
| #31 | 2.2 | 1.2 |
| #32 | 2.2 | 0.9 |
| #33 | 1.85 | 1.0 |
| #34 | 1.15 | 0.65 |
| #35 | 0.88 | 0.7 |
| #36 | 0.84 | 0.45 |
| #37 | 0.80 | 1.1 |
| #38 | 0.65 | 0.7 |
| #39 | 0.64 | 0.35 |
| #40 | 0.5 | 0.6 |
| #41 | 0.44 | 0.9 |
| #42 | 0.40 | 0.4 |
| #43 | 0.28 | 0.7 |

## DISCUSSION

The persistent and spacious chamber structures formed by leaf sheaths and their regular use by several ant species as nesting space leads us to the conclusion that *Smilax borneensis* is a myrmecophyte. The term "myrmecophyte" (or "ant-plant") is used here *sensu* Davidson & McKey (1993), i.e., the term describes plants *regularly* inhabited by ants, without implying that plants benefit from the ants. For myrmecophytes, evidence to assess fitness consequences of particular associations is often too meagre. Also, in *S. borneensis* (and other unspecific ant-plants), which can be inhabited by a variety of ant species, the outcome of the associations may vary greatly depending on the ant species involved, e.g., as in *Conostegia setosa* (Alonso, 1998) and *Zanthoxylum myriacanthum* (Moog *et al.*, in prep.).

**Specificity:** The number of ant species (18) and their taxonomic position show that the domatia of *S. borneensis* are colonized by unspecific arboreal ants. With increasing sampling effort, we expect to find still more ant species as colonizers of *S. borneensis*. The plant offers easily accessible, numerous domatia which can be occupied by a variety of arboreal ant species for nesting. The entrances into unoccupied domatia are large enough for any small to medium-sized ant visitor. In addition, the climbing habit of *S. borneensis*, growing upon trees and shrubs, and the offering of extrafloral nectar on young leaves result in a regular frequentation by a variety of visitors from neighbouring plants, thus encouraging nesting on *Smilax borneensis*. Generally, plants which provide preformed

entrances and do not restrict ant colonization by trichomes tend to have a set of opportunistic arboreal ants as inhabitants, e.g., *Ficus obscura* var. *borneensis, Clerodendrum fistulosum, Capparis buwaldae* and *Myrmeconauclea strigosa* in SE Asia (Maschwitz *et al.*, 1989, Maschwitz *et al.*, 1994a and Maschwitz *et al.*, 1994b, Maschwitz *et al.*, 1996) and *Tetrathylacium costaricense* in the Neotropics. (L. Tennant, pers. comm. in Longino & Hanson, 1995).

However unlikely, we cannot completely rule out the possibility of a specialist ant partner associated with *S. borneensis* in some parts of its distribution. For example, the facultative myrmecophyte *Conostegia setosa* (Melastomataceae) shows striking variation in ant occupation at a spatial and temporal scale (Alonso, 1998). Specificity of the ant inhabitants of *C. setosa* is variable, with occupants ranging from one obligate and a few facultative ant species in South America and up to 12 species of opportunistically nesting ant species in Central America.

Most other melastome ant-plants with leaf pouches in the American tropics lack specialized plant-ants and are instead inhabited by a range of opportunistic species (Longino & Hanson, 1995). However, non-melastome neotropical ant-plants are often associated with a small set of specialized ant partners, though the latter often share their host with opportunistic ants (Windsor & Jolivet, 1996; Longino & Hanson, 1995). The same holds for the SE Asian *Macaranga pruinosa* (Federle, 1998). This tree harbours a complex mosaic of two specialist and several generalist ant species.

**Species composition:** Ant species communities in *S. borneensis* appear to be somewhat different from other SE Asian facultative ant-plants which provide stem domatia (e.g. *Ficus obscura* var. *borneensis, Capparis buwaldae* and *Myrmeconauclea strigosa* (Maschwitz *et al.*, 1989); Maschwitz *et al.*, 1994a; Maschwitz *et al.*, 1996). For example, the *Camponotus* species of the subgenus *Colobopsis*, commonly found in the above mentioned ant-plant species, and some *Pheidole* species display nesting preferences for hollow wood and do not accept the more spacious and comparably more open leaf domatia of *Smilax*. A prerequisite for the establishment of many ant species on *Smilax* may be their ability to construct carton walls. The most common *Smilax* occupants like the *Dolichoderus* sp. (near *thoracicus*) or the *Polyrhachis* sp. can reduce the size of the entrance holes and close slits of the domatia by carton or silk carton, a behaviour typical of leaf-dwelling ants (Weissflog & Maschwitz, unpublished results). Even if such ant species are not able to build free carton nests in the foliage, their limited abilities for carton construction are sufficient for nesting in leaf domatia. Apart from producing nesting space, the ability to build carton is an efficient means to keep away predators or competitors, and may also prevent water influx. In some empty domatia of *S. borneensis*, which were twisted upside down, we could occasionally observe rain water.

**Low occupation rate of inhabitable domatia**: In general, ant occupancy rate of *S. borneensis* (59% of all domatia-bearing plants) appears to be in the usual range observed in

other facultative ant-plants. However, the occupancy rate of domatia per plant was sometimes strikingly low (minimum 2.2%, median 8.2%), and thus seems to contradict the common notion that nest space for ants in the tropics is limited. Since *S. borneensis* climbers were often very long and had numerous (sometimes inaccessible) side branches, we were not always able to check all domatia of one plant. This in part may explain the occasionally very low ant occupancy rate of domatia per plant, because most ant species collected preferred to colonise the higher sections of the climbing host. It is assumed that these ants tend to stay close to young leaves which are the sources of extrafloral nectar.

A considerable propotion of domatia of six *S. borneensis* (22%) showed signs of damage by ant predators and/or herbivores. Damage to ant-plants by predators of ants is a common phenomenon (Federle *et al.*, in press). In case of strong disturbance, facultative nesting ants, especially polydomous species, may easily shift their nest site to neighbouring plants.

Another factor influencing occupation rate is certainly the inter- and intraspecific competition both for food (extrafloral nectar) and nest sites (domatia) among ants (Kleinfeldt, 1978; Hölldobler & Wilson, 1990). This may lead to frequent stochastic disturbances which in turn may cause a strong spatial and temporal variation in ant occupancy. We suggest that high levels of disturbance, both by competing ants and predators, are the most likely reasons for the often observed low rate of ant occupation of inhabitable domatia in *S. borneensis*. Long-term studies are needed to assess species turnover in *Smilax* plants.

**Domatia**: What are the functions of these peculiar leaf sheaths? It is evident that the domatia structures of *Smilax borneensis* exist prior to the arrival of ants and are not induced by them. At most, some ants add carton to improve the shelter or to partially close the entrance. Burck (1891) argues that the "original function" of these structures is the mechanical protection of the growing buds. This appears to be plausible; however, the domatia of *S. borneensis* are persistent, hard-walled structures that probably exist as long as the associated leaf lives. We do not have any indication for a function of these structures other than housing ant after the bud has developed into a leaf.

In origin, the association of ants with *S. borneensis* (and other ant-house plants) probably is derived from the normal behaviour of arboreal ants, i.e., the ants take advantage of any suitable shelter for tending hemipterans, and/or nesting. In *Smilax*, the modification of a preformed leaf sheath structure into an ant shelter appears to be only a moderate step by increasing size, persistency and toughness.

**Myrmecophytic traits in other *Smilax* species**: Other members of the genus *Smilax* were found to have leaf sheaths that are probably well suited as ant nesting chambers. Burck (1891) mentioned three plant species with myrmecodomatia, *Smilax ovalifolia, S. indica,* and *S. zeylanica*. According to Koyama (1960), there are other *Smilax* species that possess distinct stipule-like auricles: *S. kingii, S. leucophylla, S. ocreata, S. nervo-marginata* and *S.*

*perfoliata*. With the exception of *S. ocreata, S. perfoliata,* and *S. indica* (not seen) we could not confirm myrmecophytic traits in herbarium specimens of the *Smilax* species listed by Burck and Koyama. For *S. leucophylla*, the status remains unclear. Two of 22 specimens studied in the herbarium had very small domatia-like leaf sheaths. However, they were tightly pressed to the stem and appeared to be an artifact due to the pressing and drying of the specimens. One plant found by us in the field (in Palawan, the Philippines) did not have domatia. Our herbarium studies revealed that, in addition to *S. borneensis*, three more species are likely candidates for being myrmecophytes, namely, *S. gigantea, S. perfoliata* and *A. ocreata*. Future field investigations should scrutinize results obtained from herbarium material.

## CONCLUSION

A wide set of ant species from several subfamilies regularly inhabit the stipule-like leaf sheath domatia of *S. borneensis*. Similar ant-housing structures were found in at least three more *Smilax* species, thus illustrating the potential of the genus *Smilax* to develop regular, though 'loose' associations with ants. The modification of preformed leaf-borne structures to house ant colonies appears to be a common phenomenon in many tropical plants. In the Neotropics, for instance, leaf-pouch has domatia evolved independently at least 9 times in the Melastomataceae (Davidson & McKey, 1993). On the contrary, in SE Asia leaf-pouch domatia are only known from *Callicarpa saccata* (Van Steenis, 1967).

However, other leaf-borne shelters, i.e., 'stipule-like' structures placed in pairs at the base of the petiole, roughly resembling in their appearance the domatia of *Smilax*, are less rare in the Old World tropics. Examples are African *Macaranga saccifera* (inflated, pouch like stipules), New Guinean *Psychotria myrmecophila* (stipular pouches with margins reflexed), and African *Uragoga* sp. (=*Grumilea*; swollen persistent stipules with margins recurved downwards; Bequaert, 1922; Jolivet, 1996). In an analogous case, African *Diospyros conocarpa,* persistent cataphylls are folded to form a completely enclosed domatia (Letouzey & White, 1970). Additionally, a similar type of structure is known from some species of Asian *Lepisanthes* and *Pometia* (Sapindaceae; Adema *et al.*, 1994). These plants possess pseudostipules (reduced leaflets at the base of the leaf stalk) which tightly clasp the twig. We have observed that in some species these pseudostipules are frequently used as shelters by arboreal ants (unpublished data). Another similar case was reported by Burck (1891) and Bequaert (1922) for three Asian *Fagraea* species (Gentianaceae) which bear at the base of the petiole auricle-like scales which clasp the stem. The cavities thus formed are occupied by ants which close the entrances with carton material. These old records of myrmecophytic *Fagraea* have not been confirmed to date.

In general, however, it is often not clear if such structures used as ant shelters are transformed by selection to lodge ants. Certainly, many arboreal ants only take advantage

of any suitable structure for nesting and thus would be only an epiphenomenon. As we have seen, many plant taxa have leaf-borne structures which provide the 'raw material' for the evolutionarily modification into myrmecophytic structures. We, therefore, should expect to find many plants with structures along gradient displaying variable associations with ants: from the sporadic and irregular utilization of unspecialized shelters by opportunistic ants to the regular use of real domatia by species-specific ant partners. In other words, "primitive" ant-house plants might be little different from non-ant inhabited species. But why have stipules (or analogous structures), in comparison to other plant structures such as leaf and stem, only rarely become evolutionarily modified to house ants? [The only exception are several *Acacia* species, in which thorns, themselves highly specialized stipules, function as domatia.] The principle cause may lie in the variation in cost and benefits of mutualistic associations (Bronstein, 1998). Plant shelters used by ants, such as stipule-like auricles, which do not select in some way the range of ants nesting in them (either by hairy trichomes, size of domatia or access via specialized entrances) will be utilized by members of the ant community which inevitably vary in their quality as mutualists. Strong variations in the outcome of facultative mutualisms may thus generate a complex pattern of conditions which rarely favour the evolution of specialized ant-housing structures.

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